RESEARCH ARTICLE

Botany
American Journal of

Fruit wings accelerate germination in *Anacyclus clavatus*

Rubén Torices[1] | Lucía DeSoto[2] | José Cerca[3] | Lucie Mota[4] |
Ana Afonso[4] | Cristina Poyatos[1]

[1]Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain

[2]Departamento de Biodiversidad, Ecología y Evolución, Universidad Complutense de Madrid, Madrid, Spain

[3]CEES - Centre for Ecological and Evolutionary Synthesis, Department of Biosciences, University of Oslo, Oslo 0316, Norway

[4]Centre for Functional Ecology – Science for People & the Planet, Department of Life Sciences, University of Coimbra, Coimbra, Portugal

Correspondence
Rubén Torices, Área de Biodiversidad y Conservación, Departamento de Biología y Geología, Física y Química Inorgánica, Universidad Rey Juan Carlos, Móstoles, Spain.
Email: ruben.torices@urjc.es

Abstract

Premise: The lateral membranous expansions of fruits, commonly referred to as wings, have long been theorized to serve only dispersal functions. Alternatively, because winged fruits typically have earlier seed germination than unwinged fruits, we hypothesized that wings could increase the contact surface with water, ultimately triggering earlier germination.

Methods: We investigated this alternative hypothesis by exploring the potential role of fruit wings on germination in the heterocarpic species *Anacyclus clavatus* (Desf.) Pers. (Asteraceae), which produces both winged and unwinged fruits. First, we measured the speed and degree of water absorption in winged and unwinged fruits. Second, we investigated the effects of wings on germination performance, by either reducing wing size or by preventing water absorption by sealing wings with wax. Next, we tested the influence of water availability on the germination performance of winged and unwinged fruits by reducing the water potential.

Results: Winged fruits absorbed more water at a faster rate than unwinged fruits. The sealing of wings delayed germination, whereas germination time was not significantly altered by wing cutting. The restriction of water availability by decreasing water potential significantly delayed seed germination of unwinged fruits, whereas winged fruits remained unaffected.

Conclusions: Altogether, our results support the effect of wings on germination and cast doubt on the unique role of wings in dispersal. Whether or not wings contribute to dispersal, we propose that they also improve seed germination and seedling establishment by facilitating water absorption after the release from their mother plants.

KEYWORDS
Asteraceae, bet-hedging, diaspore morphology, fruit morphology, germination activation, heterocarpy, water uptake, winter annuals

Primary dispersal vectors impose strong selective pressures, yet other ecological factors may also drive diaspore evolution (Cousen et al., 2008; Ronce and Clobert, 2012). For instance, seeds are under selective pressure to increase their overall size (Harper et al., 1970; Smith and Fretwell, 1974) because increased seed size may lead to increased germination, seedling survival, establishment, and competitive ability (Thompson et al., 1993; Andersson, 1996; Gómez, 2004; Seltmann et al., 2007). However, an increase in size generally hinders dispersal, especially for wind-dispersed diaspores (Green, 1980), establishing a trade-off between colonization and competition (Turnbull et al., 1999; Wyse and Hulme, 2022). Heterocarpic species produce two types of diaspores on the same plant. One is larger and has high competitive abilities, whereas the other is smaller and has structures facilitating wider dispersal from the maternal habitat (Dubois and Cheptou, 2012). Nevertheless, some plants in some heterocarpic species do not seem to match the expectations of this colonization–competition trade-off.

In particular, several species in the sunflower family (Asteraceae) simultaneously produce winged and unwinged fruits (Webb, 1986; Denda et al., 1999; Bastida and Menéndez, 2004). In these species, the fruits with assumed dispersal structures, namely wings, are also the heaviest, whereas the smallest fruits are unwinged (e.g., Bastida et al., 2010; Torices et al., 2013). Although it might be reasonable to assume that fruits with wings have higher dispersibilities, they are also heavier than unwinged fruits,

suggesting that these wings might play a role other than dispersal (Bastida et al., 2018). In fact, predictions of dispersal success using only the morphological traits of fruits and seeds can be misleading, since other traits, such as plant height, can be stronger determinants of dispersal success (Tackenberg et al., 2003; Augspurger et al., 2017; Thomson et al., 2011, 2018). Thus, the lateral expansions of the pericarp of winged fruits in heterocarpic species of Asteraceae might not significantly contribute to wind dispersal, and their functional significance remains unknown.

Previous studies on the heterocarpic species *Anacyclus clavatus* (Asteraceae) have shown that seeds from winged fruits germinated significantly earlier than unwinged fruits (Torices et al., 2013). This disparity in germination timing has notable implications for the fitness of the plants, as earlier germination results in larger plants and a higher yield of inflorescences, particularly under favorable and stable growing conditions (Afonso et al., 2014). This fitness advantage disappeared when germination was synchronized between winged and unwinged fruits under experimental conditions, highlighting the importance of germination time (Afonso et al., 2014). We hypothesized that wings could increase the contact surface with water, ultimately accelerating germination.

Here, we tested this hypothesis that the fast germination of seeds from winged fruits is favored by the ability of the wings to absorb water. Under this hypothesis we expect that (1) imbibition rate of winged fruits will be higher than in unwinged fruits, (2) germination time will be delayed when wings are sealed or removed, and (3) seeds from unwinged fruits will have a higher decline in germination and time than winged fruits as water potential is decreased.

MATERIAL AND METHODS

Study species

Anacyclus clavatus (Desf.) Pers. (Asteraceae) is a winter annual, self-incompatible weed in the Mediterranean Basin (Humphries, 1979; Álvarez, 2019). It produces single-seeded, dry fruits, achenes, which vary in morphology and size within the capitulum (Torices et al., 2013). Two fruit types occur in this species, winged and unwinged (Figure 1). Winged fruits always occupy the outermost positions within the capitulum, whereas unwinged fruits occupy the innermost positions (Torices et al., 2013). Moreover, fruit and wing sizes usually decrease gradually from the outer to inner positions (Torices et al., 2013). It blooms at the beginning of the spring and ripen fruits during spring or early summer. Fruits remain in their capitula and are not released until the first rains fall in autumn (Bastida et al., 2010). Fruits are released sequentially from the outermost to the innermost positions of the capitulum, so that winged fruits are the first to be released, whereas unwinged ones remain attached to mother plants longer.

FIGURE 1 Winged and unwinged fruits of *Anacyclus clavatus*.

Experimental design

We performed a set of four experiments to explore the role of wings on seed germination. First, we assessed the role of wings on imbibition rate. Second, we manipulated wings, by either sealing them (thus waterproofing them) or reducing their size by cutting wings. Third, we studied the effect of water availability by modifying water potential (ψ) on seed germination from winged and unwinged fruits, using germination media with increasing concentrations of polyethylene glycol. Lastly, we studied the effect of pericarp thickness and unopened versus manually opened pericarps on the probability o f germination.

Effects of fruit type on imbibition time

We tested whether winged fruits absorbed water at a higher rate than unwinged fruits. Fruits of both types were placed on moist filter paper at room temperatures and weighed at hourly intervals for 8 h. We selected two winged and two unwinged fruits from six different maternal plants. Fruits from each maternal plants were placed on filter paper moistened with 4 mL of distilled water in separate Petri dishes and sealed with Parafilm M to provide an environment of non-restricted water availability.

All fruits for this experiment were collected in June 2022 from a population in Central Spain (Hornillo de Cerrato, Spain, 41°58′41.04″N, 4°18′33.10″W). In the laboratory, fruits from individual capitula were separated into winged fruits (located at the outermost positions) and unwinged fruits (in the innermost positions) using a stereomicroscope. Because this species presents two flower types at the outermost positions (i.e., female and bisexual), which produce winged fruits that are slightly different in size (Torices et al., 2013) and in germination speed (Afonso et al., 2014), and because only bisexual flowers produce unwinged fruits, we used only

the outermost winged fruits produced by the bisexual flowers, located immediately after the row of female ray flowers.

We performed two imbibition tests, one with freshly matured fruits and another with fruits that were stored in the dark under room temperatures for 8 months. In this way, we tested for potential dormancy effects in freshly matured fruits or after-ripening effects (Baskin and Baskin, 2014). Fruits were weighed individually with a precision of 0.01 mg and re-weighed each hour for 8 h because fruits did not increase in mass after 6 h.

Wing experimental manipulation

We assessed the potential role of wings in water uptake through two experimental manipulations: (1) reducing wing size by cutting them and (2) waterproofing wings by sealing them with paraffin, leaving fruit body unmanipulated. For the first treatment, we cut the wings carefully with scissors, avoiding any damage to the embryo (hereafter, cut-winged fruits). Then, the fruit area was measured using ImageJ 1.50i (Schneider et al., 2012) based on images of all fruits before and after cutting their wings. When we compared the two states of each fruit, it was clear that we had effectively reduced one-third of the fruit area ($N = 120$, 32.9% ± 8.2 SD of total fruit area reduction after wing removal). Thus, the fruit area decreased significantly after wing removal ($N = 120$; mean ± SD of fruit area before cutting: 9.41 ± 2.62 mm^2; after cutting: 6.20 ± 1.49 mm^2; analysis of variance, $F_{1,238} = 135.7$, $P < 0.001$). Cutting wings might unintentionally result in an opening of the pericarp and, consequently, favor water intake by the embryo and eventually boost germination. To control for potential confounding effects of wing removal by total cutting, we introduced the second treatment, where we manipulated the potential effect of water absorption by wings by covering them with paraffin (hereafter, sealed-winged fruits). Paraffin was first liquefied by heating and subsequently spread on the wings when it had cooled down, leaving the embryo uncovered.

For this set of experiments, we used fruits collected in June 2013 after complete seed maturation and before dispersal from a population in southern Spain (Torre del Mar, Spain, 36°43′48.875″N, 4°6′ 8.154″W). We selected one capitulum from 32 different mother plants, ensuring that we had enough fruit for all experimental treatments. Collected fruits were stored dry in the dark at room temperature until the experiments were started in October 2013 when the germination window usually begins in its native population.

To compare the germination performance of experimental (cut or sealed winged) and control (winged and unwinged) fruits, each of the four types was placed on filter paper moistened with 4 mL of distilled water in the same Petri dish. For each of the 30 maternal plants, we included four Petri dishes, totaling 480 fruits. Each Petri dish was sealed with Parafilm M to provide an environment of nonrestricted water availability. The Petri dishes were placed in a climatic chamber (Fitoclima D1200 PLH; Aralab, Rio de Mouro, Portugal) at the University of Coimbra at 25°C, with 75% relative humidity, 16 h of light, and 8 h of darkness. Germination was monitored daily during the first 24 days, every 2 days until the 70th day, and weekly thereafter. The experiment ran for 209 days, from 8 October 2013 to 6 May 2014. Germination probability and mean germination time were estimated after 209 days, i.e., the duration of the germination experiment. Germination speed was estimated as the slope of the relationship between germination time and probability as fitted by time-to-event parametric models (see below).

Effects of water availability on germination performance

We explored the germination performance of winged and unwinged fruits under experimental conditions by changing water availability. To restrict water availability, we modified the water potential (ψ) of fruits a series of increasing concentrations of polyethylene glycol (PEG) 8000 (Michel, 1983). We set four water potential environments, from 0 to –1.5 MPa, using the following PEG concentrations in distilled water: $\psi = 0$ MPa ([PEG 8000] = 0 g L^{-1}); $\psi = –0.5$ MPa ([PEG 8000] = 60.20 g L^{-1}); $\psi = –1.0$ MPa ([PEG 8000] = 96.32 g L^{-1}); $\psi = –1.5$ MPa ([PEG 8000] = 117.97 g L^{-1}).

Fruits for this experiment came from the same population as the wing manipulation experiment described above. To ensure a broad genetic background, 16 winged and 16 unwinged fruits were selected from 28 maternal plants, totaling 896 fruits. For each maternal plant, we set up four Petri dishes, representing the four different water potential levels (0, –0.5, –1.0, and –1.5 MPa). Within each Petri dish, we carefully placed four fruits of each type (winged and unwinged), all originating from the same maternal plant. This design ensured that each maternal plant was replicated four times, corresponding to each water potential level, while maintaining both types of fruits within each Petri dish. All Petri dishes were placed in a chamber with the same temperature, light, and humidity and monitored using the scheme described for the wing experimental manipulation (see above).

Pericarp opening test

To better understand the potential effects of the wing cutting treatment, we performed an additional experiment using winged and unwinged fruits in which the pericarp was slightly cut to favor embryo water uptake. Using a scalpel, we incised the pericarp in the distal upper part of fruits without touching the embryo or wings, and a tetrazolium test after germination confirmed that most of the embryos were not damaged by the pericarp cutting. Fruits for this experiment were selected from the same population and maternal plants as the imbibition test. For 10 maternal plants, we experimentally cut the pericarp in 10 unwinged

and 10 winged fruits. These fruits were placed on filter paper moistened with distilled water in the same Petri dish together with control unwinged ($N = 10$) and winged ($N = 10$) fruits. Each Petri dish was sealed with Parafilm M to provide nonrestricted water availability. All Petri dishes were placed in a climatic chamber (Estufa F-1, Ibercex, Arganda del Rey, Spain) at King Juan Carlos University in the same conditions used for the previous germination tests. The experiment began on 11 July 2022 and ran 2 weeks until 26 July 2022. On the same day, we tested the viability of nongerminated seeds by cutting seeds transversally and placing them in 1% w/v aqueous tetrazolium for 3 h at 30°C; live tissues stain red, and dead tissues are not stained (Baskin and Baskin, 2014).

Pericarp thickness

To assess whether winged and unwinged fruits differ in pericarp thickness, we cut and measured 27 fruits of each type (winged or unwinged) from nine different maternal plants of the same population used for imbibition testing and the pericarp opening experiment. Fruits were transversally cut in the middle, photographed with a stereomicroscope, and pericarp thickness measured using ImageJ (Schneider et al., 2012).

Statistical analyses

Data were analyzed using general or generalized linear mixed models (GLMM), using the R package lme4 (Bates et al., 2015) and R 4.0.3 (R Core Team, 2020). In all models, statistical differences between treatment levels were assessed using least-square mean differences, using the R package emmeans (Lenth, 2020), and P-values for these post hoc comparisons were corrected using Holm's adjustment.

Imbibition rate was assessed by means of a linear mixed model with the increase in mass as a percentage of the initial mass as the response variable. Fruit type, after-ripening status, and time were included as explanatory fixed variables; fruit identity, Petri dish, and maternal plant were added as random variables.

For the experiments in which we manipulated wings and water availability, we fitted models for the probability of germination and germination time with maternal plants and Petri dishes nested in maternal plants included as random factors. Specifically, the probability of germination was modeled using a binomial distribution with a logit link function, and the time of germination was modeled using a negative binomial distribution with a log link function. For the wing manipulation experiment, there was only one fixed factor, which was the fruit type (winged, unwinged, cut, and sealed-winged). Whereas for the water availability experiment, the model included the effect of fruit type (winged vs. unwinged), water potential, including its interaction.

In addition, for these two experiments, germination rates were also assessed by fitting an accelerated failure-time model using the R package survival (Therneau, 2020). We used the maximum likelihood approach and log-logistic distribution (Fox, 2001). For the wing manipulation experiment, one model was fitted, including the experimental treatment and maternal plant as explanatory variables. For water availability experiment, we fitted one specific model for winged and unwinged fruits to explore whether water potential led to different germination rates for each fruit type, accounting for the maternal plant. To explore the effect of fruit size, we also assessed the effect of the ratio of fruit area to fruit weight on germination probability and mean germination time and speed.

Pericarp thickness was also analyzed fitting a linear mixed model with pericarp thickness as the response variable, fruit type as the explanatory variable, and maternal plant as a random variable. The effect of experimentally opening the pericarp on the probability of germination and seed viability were assessed for winged and unwinged fruits using a binomial distribution with a logit link function. Both models included the effect of fruit type (winged vs. unwinged) and pericarp opening treatment, including its interaction. Petri dish was included as random variable.

RESULTS

Effects of fruit type on imbibition time

Anacyclus clavatus fruits quickly increased in mass on moist paper (Figure 2; Appendix S1). The increase in mass was disproportionally larger (fruit type main effect: $N = 384$,
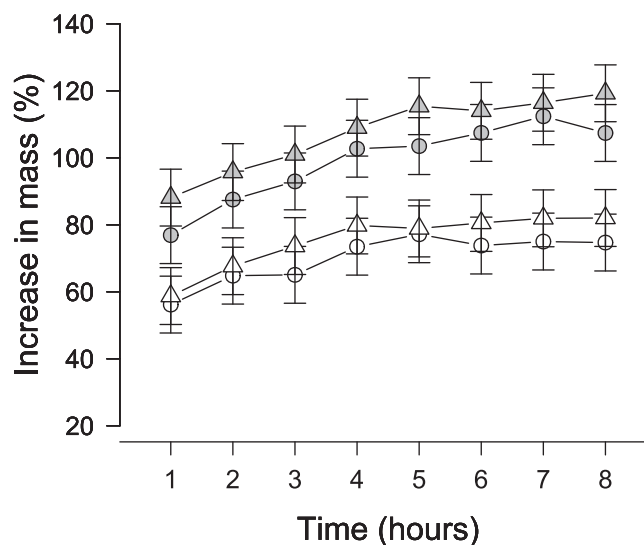

FIGURE 2 Effects of winged morphology and after-ripening on imbibition rate. Least square means (±95% CI) of percentage increase in mass of winged (grey symbols) and unwinged (white symbols) fruits containing freshly matured (triangle) and after-ripened (dots) seeds of *Anacyclus clavatus*.

$\chi^2 = 13.0$, $P < 0.001$; Figure 2) in winged than unwinged fruits. The largest increment in mass was produced within the first hour (Figure 2) when winged fruits had a significantly faster increment in mass than unwinged ones (non-overlapping 95% CI; Figure 2). After-ripening of *A. clavatus* fruits significantly decreased water uptake irrespectively of their morphology ($N = 384$, $\chi^2 = 348.4$, $P < 0.001$; Figure 2).

Effect of wing manipulation on germination

Paraffin wing sealing reduced the probability of germination and prolonged the germination time (Figure 3A, B; Appendix S2, Table S1), leading to an unwinged-like germination delay in seeds of sealed-winged fruits (Figure 3C; Appendix S2, Table S2). Germination was not significantly altered by cutting the wings compared with the results obtained for the winged fruits (Figure 3C).

Effects of water availability on seed germination from winged and unwinged fruits

Seeds of winged fruits had a higher probability of germination and a shorter mean germination time than those of unwinged fruits under all water potential conditions (Table 1, Figure 4A, B). A decrease in water potential reduced the germination probability of seeds from both fruit types (Table 1). Nevertheless, a decrease in water potential had a differential effect on the mean germination time of seeds of winged and unwinged fruits, as indicated by the significant interaction between fruit type and water potential (Table 1). Water potential did not affect the mean germination time in winged fruits (Figure 4B), but a reduction in water potential led to an increase in the mean germination time in unwinged fruits (Figure 4B). This differential effect on germination was particularly pronounced when comparing the germination curves (Figure 4C, D; Appendix S3). A decrease in the water potential significantly reduced the germination speed of seeds from unwinged fruits (Figure 4D), whereas for winged fruits, we found only a slight nonsignificant reduction in the germination rates (Figure 4C).

Wing size showed an independent effect of fruit size because the ratio of fruit area to fruit mass significantly affected both germination probability and time (Appendices S4 and S5). Those seeds from fruits with a high fruit area to fruit mass ratio germinated significantly earlier and faster than seeds from fruits with a low ratio (both $P < 0.001$; Appendix S5). In addition, there was a significant interaction between water potential and fruit area to mass ratio on germination time ($P = 0.009$; Appendix S4). As water potential decreased, seeds in fruits with a low area to mass ratio showed delayed germination times relative to seeds in fruits with a high ratio (Appendix S5).

TABLE 1 Effects of water potential on germination probability and germination time of seeds of winged and unwinged fruits.

Variables	N	df	χ^2	P
Germination probability	889			
Water potential (WP)		3	12.76	0.005
Fruit type (F)		1	98.12	<0.001
WP × F		3	4.77	0.190
Germination time	632			
Water potential (WP)		3	7.54	0.056
Fruit type (F)		1	45.55	<0.001
WP × F		3	8.54	0.036

Notes: The interaction between water potential (0 MPa, –0.5 MPa, –1.0 MPa, –1.5 MPa) and fruit type (winged vs. unwinged) was assessed using type III tests. When the interaction was not significant, the main effects were assessed using type II tests. Maternal plants and Petri dishes nested in maternal plants were included as random factors in all models.
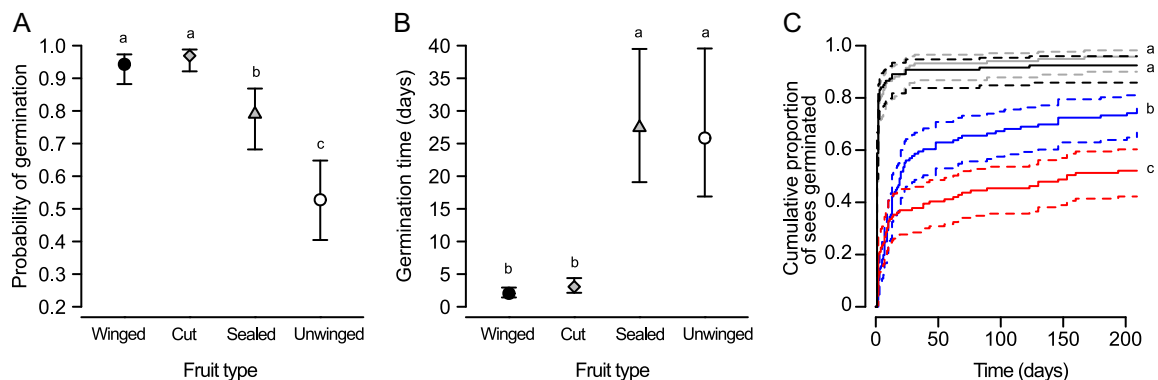

FIGURE 3 Effect of wing manipulation on germination. Least-square means (±95%) of (A) probability of germination and (B) germination time of seed of winged (black dots), cut-winged (grey diamonds), sealed-winged (grey triangles), and unwinged (white dots) fruits of *Anacyclus clavatus*. (C) Accumulated germination curves and 95% CI for seeds of winged (black), cut-winged (grey), sealed-winged (blue), and unwinged (red) fruits. Different letters indicate significant differences between treatment levels ($P < 0.05$).
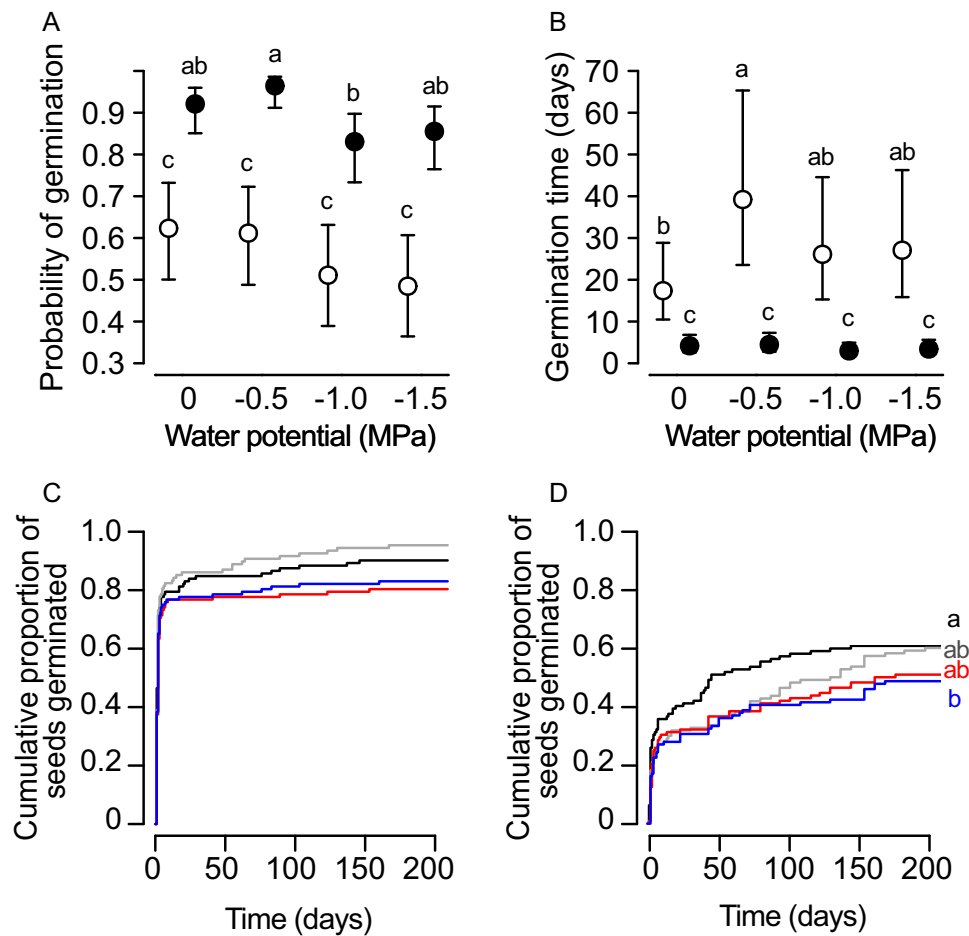
FIGURE 4 Germination in different water availability environments. Least-square means (±95%CI) of (A) probability of germination and (B) germination time of seeds of winged (black) and unwinged (white) fruits of *Anacyclus clavatus*. Accumulated germination curves of seeds of (C) winged and (D) unwinged fruits for each water availability environment: $\psi = 0$, black line; $\psi = -0.5$, grey line; $\psi = -1.0$, red line; and $\psi = -1.5$, blue line. Different letters indicate significant differences between treatment levels ($P < 0.05$).

Pericarp thickness and pericarp opening test

Unwinged fruits had significantly thicker pericarp than winged ones ($N = 58$, $\chi^2 = 8.59$, $P = 0.003$, Figure 5A). Experimental pericarp opening significantly increased the probability of germinated seeds from both winged and unwinged fruits (Figure 5B; Appendix S6). Freshly matured fruits were used for this experiment, and a low percentage of seeds germinated (Figure 5B). Pericarp opening did not reduce seed viability (Figure 5C), and most of these nongerminating seeds were still viable as indicated by the tetrazolium test (Figure 5C; Appendix S7).

DISCUSSION

The lateral membranous expansions of fruits, usually called wings (e.g., Humphries, 1979; Cron et al., 2009; Bello et al., 2013), have long been believed to exclusively serve dispersal functions (e.g., Manchester and O'Leary, 2010). In *A. clavatus*, we herein show that these wings (Figure 1) play

a significant role in water absorption and, thus, in germination activation. Therefore, wings may not only contribute to seed dispersal, but also improve seed germination and seedling establishment after their release from the maternal plants.

Our results unequivocally support the role of wings in water absorption and link the wings to germinability. They are also consistent with previous evidence showing the influence of pericarp anatomy on germination (Imbert, 2002). The lateral membranous expansions of *A. clavatus* fruits increase the fruit area, thus extending the surface through which water and gases could enter the embryo to initiate germination. The experimental manipulation in this study, which involved sealing wings with paraffin, supported the hypothesis of increased absorption ability because germination of seeds from sealed fruits was significantly reduced and slower compared to seeds from unmanipulated winged fruits. Furthermore, wings on fully imbibed fruits may help to retain water longer than in unwinged fruits, keeping the embryo moist, which may be critical in more restricted natural conditions. In the
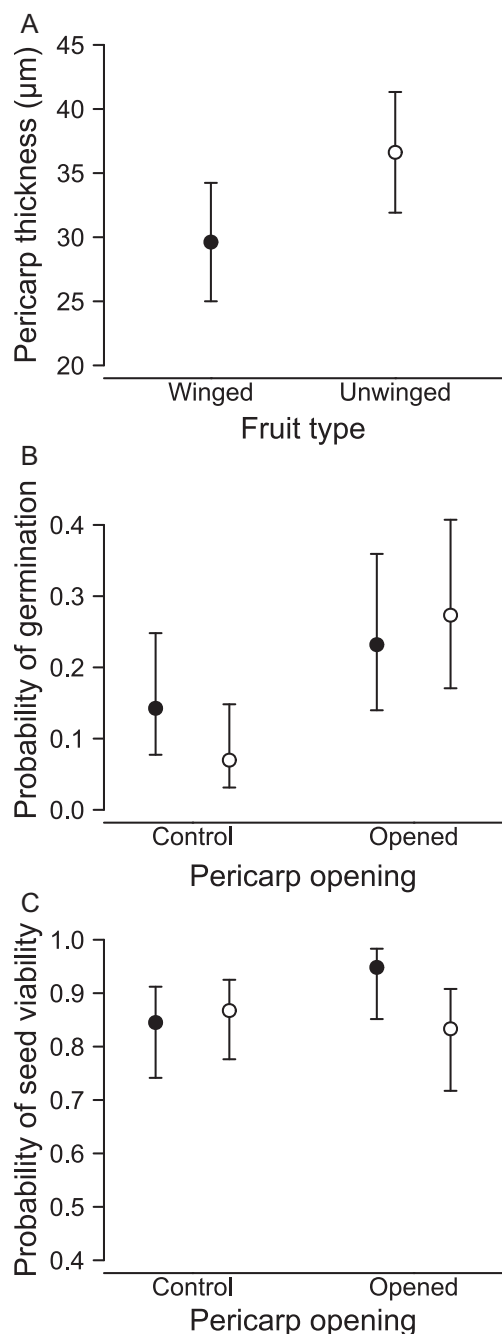
FIGURE 5 Pericarp thickness and the effect of experimental pericarp opening in the probability of seed germination and seed viability of *Anacyclus clavatus* fruits. Least-square means (±95% CI) of (A) pericarp thickness ($N = 27$ for each fruit type), (B) probability of germination ($N = 100$ for each group), and (C) probability of viability ($N = 83, 60, 71$, and 58 for control winged, control unwinged, opened winged, and opened unwinged fruits, respectively) of seeds of winged (black dots) and unwinged (white dots) fruits of *Anacyclus clavatus*.

experiment in which we simulated water scarcity by decreasing water potential, germination of seeds of winged fruits was similar to that in the favorable control conditions, whereas germination of seeds of unwinged fruits was reduced. Hence, all these experimental manipulations support that water availability might be a critical cue for

A. clavatus embryo activation and that wings might promote germination of nondormant seeds.

Conversely, when wings were cut, the germination probability and speed were as high as in the control winged fruits. Although we meant to reduce water absorption by wing removal, the cutting process might have produced the opposite effect and favored embryo imbibition by the effect of pericarp opening. In fact, our test of pericarp opening supports this side effect of wing cutting, because early germination significantly increased in those fruits whose pericarps were experimentally opened (Figure 5).

Despite the effect of wings in accelerating germination, the observed differences in seed germination times between winged and unwinged fruits cannot be exclusively attributed to the presence of wings. The delayed germination time and lower percentage of germination of seeds from unwinged fruits in our tests were likely also to be the consequence of dormancy variation between types of fruit morphologies. After pericarps were experimentally opened, seed germination of both types of fruits increased, suggesting a negative effect of pericarp thickness on germination. Furthermore, thicker pericarps of unwinged than winged fruits might increase seed germination time through mechanical restriction on the embryo, consistent with the previous evidence that thick pericarps restrict gas exchange and water absorption to embryos (McEvoy, 1984; Tanowitz et al., 1987; Prinzie and Chmielewski, 1994). In addition, the low germination probability despite the high viability observed in seeds of freshly matured fruits supports that this species could require after-ripening during the summer to break dormancy (Baskin and Baskin, 1990; Bewley, 1997; Finch-Savage and Leubner-Metzger, 2006). However, the similar seed germination for both types of fruits when freshly matured suggests that they have similar levels of physiological dormancy. Therefore, the longer germination times of seeds from unwinged fruits cannot be attributed only to the lack of wings, since their thicker pericarps may impose a higher mechanical restriction than in winged fruits. To rule out the effect of wing absence in the delayed germination of seeds of unwinged fruits, we need to experimentally separate wing presence/absence from the confounding effect of seed dormancy.

As wing and fruit sizes are correlated in *A. clavatus*, the contribution of wings to germination could be confounded by size effects. In fact, heavier fruits and winged morphology jointly contribute to better germination performance in *Anacyclus* spp. (Torices et al., 2013). Our experiment, however, allowed the separation of morphological effects from size effects, as wing sealing significantly delayed the germination of winged fruits. Additionally, we observed that the ratio of fruit area to fruit mass significantly increased both germination probability and time (Appendices S4 and S5), supporting that the larger relative proportion of fruit surface area in winged fruits than in unwinged fruits can be an important trait for germination in this species. Wings might enhance water absorption through enlarged surface area and reduced pericarp thickness, consequently promoting germination.

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The contribution of wings to seed germination rather than dispersal may reconcile the heterocarpy of *A. clavatus* according to the bet-hedging theory. The high/low-risk bet-hedging strategy predicts that larger seeds, which require greater resource investment, should remain closer to maternal plants, where the microenvironment is theoretically more predictable, but competition is expected to be higher (Venable and Brown, 1988). Furthermore, smaller seeds should be dispersed to new environments, where the risk of facing less-suitable habitats is higher (Venable and Brown, 1988; Imbert, 2002). Thus, under the assumption that the main role of wings is dispersal, an association between larger wings and lighter fruits is expected, whereas larger fruits should lack dispersal structures.

Alternatively, the presence of wings in the heterocarpy of *A. clavatus* might be related to seed dispersal over time rather than space. Although we did not test for the effect of wings on the effective dispersal of this species, some doubts have been raised regarding the efficiency of these structures in wind dispersal, given the low height of this plant and the mechanisms of fruit release associated with rainfall (Torices et al., 2013). A recent study on a close relative, the winged-fruited, heterocarpic herb *Pallenis spinosa*, showed that winged fruits were not dispersed farther than unwinged fruits (Bastida et al., 2018). In the shrub *Brandisia hancei*, winged seeds do not disperse farther than experimentally unwinged seeds, but they float better and attach better to substrates than unwinged seeds do (Ren et al., 2021). *Anacyclus clavatus* is a winter annual with an aerial seed bank, and the seeds are sequentially released with autumnal rains (Bastida et al., 2010). The earliest fruits to be released are the winged fruits. Those seeds germinating faster might occupy empty places and thus compete with the neighboring conspecifics (Afonso et al., 2014). Production of larger seeds will positively affect seedling competition, and the lack of dispersal by winged fruits may guarantee that offspring stay within similar microhabitats to those occupied by the maternal plants. Seeds from unwinged fruits are released later and require more time to germinate, possibly representing a source of seedlings to occupy the remaining available habitats or replace early mortality in the first-established seedlings as a bet-hedging strategy.

Names for specific traits that suggest a particular function may sometimes be misleading regarding the actual roles of those traits. In the specific case of lateral membranous expansions of the pericarp of *A. clavatus* fruits, usually called wings, we have shown that they play an important role in triggering germination, which can be a crucial process in seedling establishment and subsequent plant competition and performance.

AUTHOR CONTRIBUTIONS

R.T. and L.DS. conceived the research. All the authors designed and executed the experiments. R.T. analyzed the data and wrote the first draft. All authors provided critical comments on the drafts and read and approved the final version of the manuscript.

ORCID
Rubén Torices http://orcid.org/0000-0001-9604-1111
Lucía DeSoto http://orcid.org/0000-0002-5814-5865
José Cerca http://orcid.org/0000-0001-7788-4367
Lucie Mota http://orcid.org/0000-0003-2768-461X
Ana Afonso http://orcid.org/0000-0002-2920-2699

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Effects of fruit type and after-ripening on imbibition rate.

Appendix S2. Effects of wing manipulation on germination.

Appendix S3. Type II effects of the accelerated failure-time model (log-logistic distribution) for germination speed of winged ($N = 444$) and unwinged ($N = 445$) fruits in different water potential environments.

Appendix S4. Effects of the ratio between fruit area, fruit mass, and water potential on germination probability and time for seeds from winged and unwinged fruits.

Appendix S5. Effect of the ratio of fruit area to fruit mass on germination time in different water availability environments.

Appendix S6. Type III effects of pericarp opening on germination probability in both winged and unwinged fruits. Maternal plant ($N = 10$) was included as a random factor.

Appendix S7. Type III effects of pericarp opening on seed viability in both winged and unwinged fruits. Seed viability was assessed with the tetrazolium test. Maternal plant ($N = 10$) was included as random factor.